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Constant eyespot display as a primary defense – survival of male and female emperor moths when attacked by blue tits

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Abstract. Large conspicuous eyespots, commonly found on the wings of butterflies and moths, have been shown to thwart attacks from predators. Previous experiments have focused on lepidopteran species that expose eyespots only when harassed by a predator. In contrast, we investigate the potential efficiency of the constantly exposed eyespots of emperor moths thus constituting a primary defense. We staged experiments between blue tits and moths having either intact or painted over eyespots. Moths with eyespots were killed as often as moths without eyespots and were, additionally, approached earlier by the birds suggesting that birds were not intimidated by their eyespots. Female moths weighed three times more than males and were less often eaten, suggesting that their large size intimidated the birds. We suggest that the constant eyespot display of the emperor moth may be associated with a cost, because potential predators seem to be attracted rather than intimidated by the display.

Key words: Eyespots, predation, anti-predator behavior, emperor moth.

Introduction

Through the pressure of predation, prey animals have evolved a variety of traits that permit them to avoid detection and subsequent attack by predators. Edmunds (1974) divided these adaptations into primary defenses, having the purpose of decreasing the risk of being attacked in the first place, and secondary defenses that operate during actual encounters with a predator. Examples of primary defenses include classical concepts like crypsis, aposematism and mimicry (e.g. Cott, 1940; Endler, 1981; Ruxton *et al.*, 2004), and secondary defenses include, for example, different flight behaviors, various forms of retaliation such as stings and toxins, and also different forms of intimidating or deimatic behaviors (e.g. Humphries & Driver, 1971; Edmunds, 1974).

A trait often associated with intimidation is large and conspicuous eyespots that, to a human observer, resemble the vertebrate eye (Poulton, 1890; Cott, 1940; Blest, 1957; Ruxton, 2005). Eyespots can be conveniently defined as the presence of concentric rings of contrasting colour surrounding a central pupil (Kodandaramaiah *et al.*, 2009); it is a trait that is common on the wings of butterflies, moths and other insects, and also occurs in other animal groups, such as tropical fish, frogs, and birds (Cott, 1940; Blest, 1957; Edmunds, 1974). Large conspicuous eyespots on the wings of Lepidoptera have been hypothesized to function in two different ways (1) either by intimidating predators by creating the illusion that the predator's own enemy has suddenly appeared (the "intimidation hypothesis") or (2) or by being inherently intimidating due to their conspicuous and contrasting features (the "conspicuous signal hypothesis"; Poulton, 1890; Cott, 1940; Blest, 1957; Tinbergen, 1958; Ruxton *et al.*, 2004; Stevens, 2005, 2007; Stevens *et al.*, 2007). Although these hypotheses have been considered for over a century, support for these ideas are largely lacking (Ruxton *et al.*, 2004; Stevens, 2005), and only recently have the eyespots

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of the edible peacock butterfly (*Inachis io*) and the peacock pansy (*Junonia almana*) been shown to thwart predator attacks (Vallin *et al.*, 2005, 2006, 2007; Kodandaramaiah *et al.*, 2009). Recent field studies on spotted artificial prey have indicated that spot pattern features such as larger size and high internal pattern contrast are important for reducing predation, whereas spots occurring in pairs are no better than three spots or a single spot if they occupy the same total area (Stevens *et al.*, 2007, 2008a).

Large and conspicuous eyespots on the wings of butterflies and moths can either be hidden from view when the insect is resting, as in *I. io* and the eyed hawkmoth (*Smerinthus ocellatus*) or they can be displayed at all times, including when the insect is resting, as in the emperor moth (*Saturnia pavonia*). In the former case, the large conspicuous eyespots are exposed suddenly, only when a predator comes near, and conceivably can create a startling effect that effectively thwarts predator attacks, and hence represents a secondary defense (Blest, 1957; Edmunds, 1974; Ruxton *et al.*, 2004; Vallin *et al.*, 2005). It appears, however, that the antipredator efficiency of suddenly exposed large eyespots may be contingent on the behavior of the insect: when attacked by a bird the peacock butterfly suddenly opens and closes its wings in a repeated sequence and also tracks the movements of the attacking bird which creates the impression that the butterfly is actively defending itself. This antipredator behavior is very effective and recent experiments showed that 43 out of 44 peacocks with intact eyespots survived attacks by blue tits (*Cyanistes caeruleus*) (Vallin *et al.*, 2005, 2006). When the hawkmoth *S. ocellatus* is attacked it suddenly lifts its cryptic forewings thereby exposing the two large eyespots on the hind wings, and then moves rhythmically up and down continuously displaying its eyespots. This antipredator behavior seems to be less effective and experiments have shown that only 6 out of 27 eyed hawkmoths survived attacks from blue and great tits (*Parus major*) when the bird and lepidopteran interacted during 30-minute trials (Vallin *et al.*, 2007).

The conspicuous eyespots on the wings of a resting *S. pavonia* are constantly exposed and so cannot exert a startling effect, but when attacked the moth raises its forewings thereby exposing the hind wings which also bear eyespots that are identical in size and shape to those on the forewings (Fig. 1). Hence, the eyespots on the forewings represent a primary defense potentially deterring predators from attacking, whereas the sudden exposure of the eyespots on the hind wings represents a secondary defense that may make the predator abort its attack in progress (Cott, 1940; Ford, 1955; Edmunds, 1974). Recently, the constant exposure of large conspicuous eyespots on the wings of *J. almana* were shown to elicit fear symptoms in attacking Great tits (*Parus major*) in an experiment, and when choosing between attacking a mounted butterfly with its eyespots intact or painted over, the birds attacked the eyespotless butterflies more often (Kodandaramaiah *et al.*, 2009). However, the combined effect of eyespots as a primary, and a secondary defense has never before been tested in a living lepidopteran.

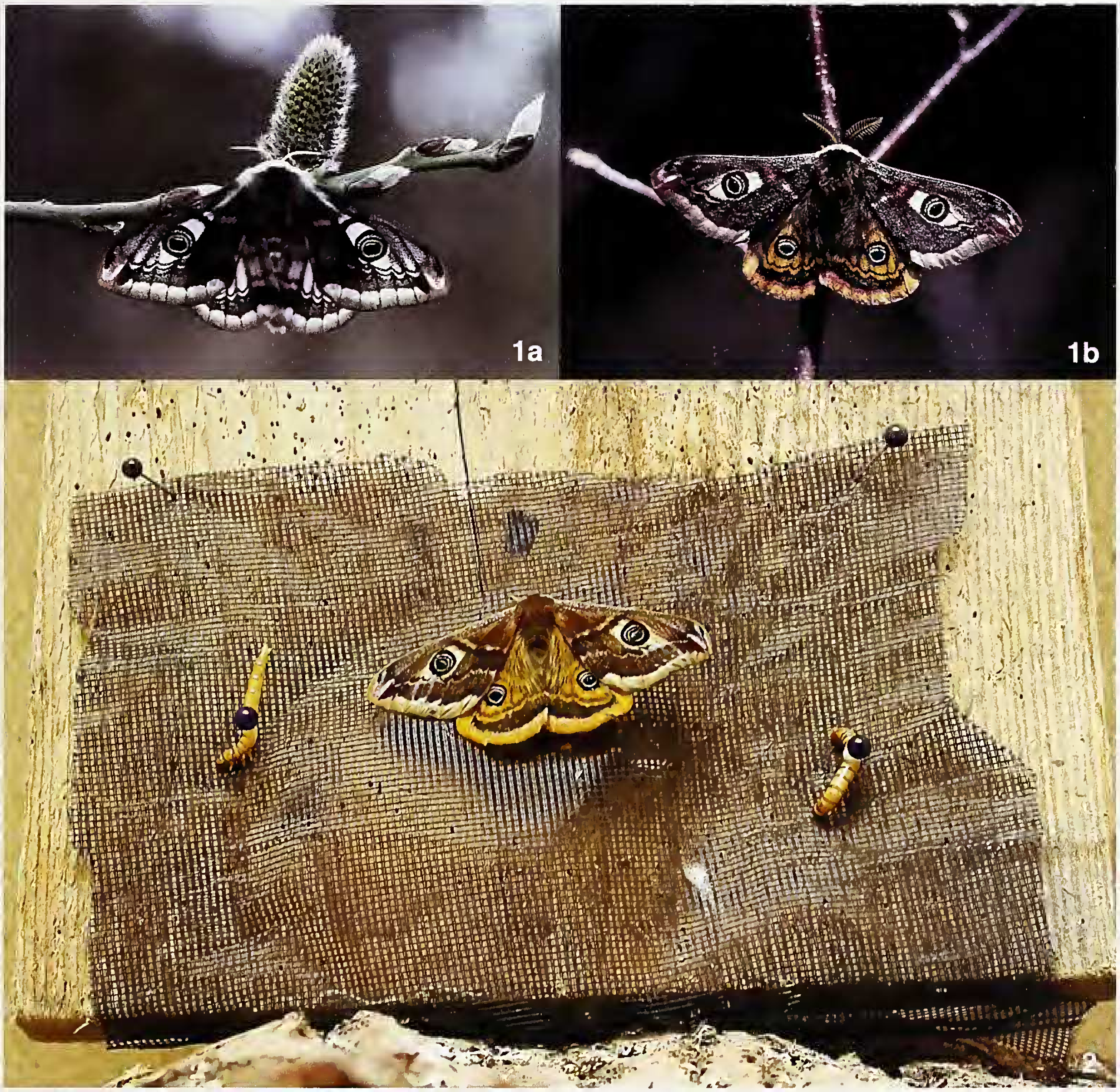
Another factor that is relevant when considering interactions between predators and potentially intimidating prey is the size of predator relative to prey. Indeed, Tinbergen (1958) pondered the possibility that an insect as big as *S. ocellata* might be too big a food item for a small passerine, and female *S. pavonia* are just as big as *S. ocellata*.

Hence, it is conceivable that large size of the insect prey itself can to some degree exert an intimidating function. In this context it is noteworthy that *S. pavonia* is sexually dimorphic both with respect to size, the males are approximately three times smaller than the females (see results), and whereas the hind wings of females are the same color as the forewings the male hind wings are bright orange red. This means that if size is an intimidating factor, female *S. pavonia* would be better defended against small passerines than males, whereas the opposite effect would be expected if red coloration exerts a strong warning effect, red coloration being typically associated with aposematic defense in insects (Ruxton *et al.*, 2004).

In this paper we address two issues: (1) whether the constantly displayed eyespots on the wings of *S. pavonia* thwart attacks by blue tits; we do this by staging experiments with living birds and moths that are either un-manipulated, have their eyespots painted over, or have been sham-painted on the basal parts of their wings leaving their eyespots intact, and (2) whether large size of the insect prey, or red hind wing coloration, can be effective as an anti-predation device; we do this by presenting the birds either male or female emperor moths.

Methods

The two species used in these experiments, the prey, the emperor moth (*Saturnia pavonia*), and the passerine predator, the blue tit (*Cyanistes caeruleus*), both have a Palearctic distribution and so are largely sympatric (Rougeot & Viette, 1980; Perrins & Snow, 1998). Blue tits are opportunistic predators feeding on both seeds and insects; however, they feed their young exclusively insects which implies good insect



Figures 1-2. **1a**. A female emperor moth (*Saturnia pavonia*), in its resting posture constantly displaying the two conspicuous eyespots on the forewings. **1b**. A male emperor moth that after being disturbed has protracted its forewings and thereby displays also the two eyespots on the red-orange hind wings. **2**. A male small emperor moth sitting on a piece of gauze netting that was attached to a plank resting against the wall of the experimental room. To ensure consistent presentations, emperor moths were always placed over a small mark on the plank (not visible in the photo). To speed up trials, two mealworms were attached to the plank at a short distance from the moth.

catching skills (Gosler & Clement, 2007).

All trials were carried out at Tovetorp Zoological Research Station, located in the southeast of Sweden, approximately 90 km south of Stockholm. Blue tits were captured, outside their breeding-season, with mist-nets in the research station's surroundings (permit 619:M03 Swedish Bird Ringing Centre). They were housed individually in indoor cages (80 x 60 x 40) cm equipped with perches for the birds to rest upon. In the cages, the blue tits had *ad libitum* access to water, sunflower seeds (*Helianthus annuus*), suet and mealworms (*Tenebrio molitor*). Experimental setup and procedures and housing of the birds were reviewed and approved by the regional ethical committee (permit Linköpings djurförsöksetiska nämnd 49-01). After the completion of a trial, birds were banded, using rings from the Swedish Bird Ringing Centre, to enable future identification and to assure that a specific individual was never used in more than one trial. Birds were then released at the site of their capture. No bird was kept in captivity for more than a week. All birds maintained their condition during captivity and were healthy upon release.

Pupae of emperor moths, *Saturnia pavonia*, were obtained from Worldwide Butterflies Ltd. After eclosion, the emperor moths were kept in plastic cups, sitting on a piece of gauze netting stretched over the cup. The emperor moths were then transferred to a cool storage room (6°C) where they were kept until the time of the experiment.

The experimental protocol of this study consisted of five different treatments. One group of male emperor moths were left unmanipulated (male-unmanipulated), a second group (male-no eye) had their four eye-spots on the dorsal side of their wings covered with water-based grey acrylic-paint (Marabu Decormatt) and the third group (male-eye) was sham-painted on the basal part of their wings so as to leave their eyespots intact. In a similar manner, females were either left unmanipulated (female-unmanipulated) or had their eyespots covered with acrylic paint (female-no eye). Unfortunately, too few females eclosed to create a treatment with sham-painted individuals with their eyespots intact. The experiments in this study were performed on two occasions. Experiments with unmanipulated male and female emperor moths were conducted during February through early April 2005. Using the same experimental setup we performed the experiments on the painted emperor moths (male-eyes, male-no eyes, female-no eyes) in February and March 2007.

Trials were carried out inside a small room (2.3 x 2.4 x 1.9) m with one-way windows on two of the walls that allowed us to observe the interactions between a bird and an emperor moth without disturbing them. The room was lit by six daylight fluorescent tubes. A longitudinally cut log of sallow (*Salix caprea*) was placed on the floor so that one of its cut of ends was in contact with one of the walls. At the other end of the log, a water bowl was placed on the floor to allow birds free access to water during a trial. On top of the log, a rough plank (80 x 20) cm was placed against the wall in a vertical position. Before a trial began, randomly a female or a male small emperor moth was transferred from its plastic cup, still sitting on the piece of gauze netting, to the plank. This was done by pinning the net to the plank using map pins. To enable consistent presentations, the emperor moth was always placed over a small mark on the plank, situated 10 cm above the log. To mimic their natural resting position, the small emperor moth was placed head up in the experimental room. On both sides of the emperor moth, at a distance of approximately 4 cm, a mealworm was attached to the board using a map pin (Fig 2.). The function of the mealworms was to speed up the trials by encouraging the birds to approach the experimental set up.

A trial began with a bird being let into the experimental room by a small hatch in the door. We noted the time when the bird first visited the log and also the time to the first attack on either mealworm. Additionally, we measured the time elapsed until the bird executed its attack on the emperor moth. A trial lasted a maximum of 30 minutes but ended earlier if a bird killed and consumed an emperor moth. To get a crude indication of the palatability of the emperor moths, blue tits were always allowed to finish eating a seized insect before the trial was ended. All trials were observed directly and, additionally, recorded using a digital videocamera (Sony DCR-VX1000E). The video recordings allowed us to review trials and were also used to establish whether a bird made physical contact or merely performed an intention movement towards the emperor moth during a specific attack, something that would be difficult to differentiate between through direct observation.

To quantify the size difference between sexes, the left forewing of nine dead females and 14 dead males were measured using a plastic ruler with a millimeter scale. Furthermore, we weighed 13 females and 10 males within a few hours of eclosion on an electro balance to quantify the difference in mass between sexes.

Statistical analysis

All statistical tests are two-tailed and were conducted using Statistica for Windows 5.5 (StatSoft Inc.). All values given are mean ± SE. Data on time to the first visit by birds on the log on the floor were log-transformed to achieve homogeneous variance in the different treatments. Non-parametric tests were used when analyzing data with more skewed distributions.

Results

The five treatments did not differ in time to when the birds first visited the log with the emperor moth (ANOVA $F_{4,50} = 2.1$, $p = 0.10$, see Table 1 for sample sizes and mean values). Similarly, there was no difference in time to the first actual attack on the emperor moths in the different treatments (ANOVA $F_{4,35} = 0.51$, $p = 0.73$). Finally, there was no difference between treatments in the number of attacks performed by the birds during the 30–minute trials (Kruskal-Wallis test: $H_4 = 5.47$, $N = 60$, $p = 0.24$). Hence, the birds attacked emperor moths with eyespots as soon and as frequently as moths without eyespots, which suggests that they were not intimidated by the conspicuous eyespots. Moreover, after 30 minutes of interacting with the blue tits 50% of the emperor moths in the treatments male-eyes (6 of 12) and male-no eyes (6 of 12) were still alive and thus there was no difference in survival. Furthermore, there was no difference in the number of times blue tits approached male-eyes (6.8 ± 1.8, N = 12) compared with male-no eyes emperor moths (9.7 ± 2.5, N = 12) (Mann-Whitney U-test: $U = 58$, $p = 0.44$). Accordingly, having eyespots did not confer any survival advantage to male emperor moths in our experiments.

Pooling the data on male and female emperor moths in treatments with or without eyespots, respectively, birds were found to visit the log on the floor after a shorter time in trials with emperor moths with eyespots (male-eyes, male-unmanipulated, female-unmanipulated) (171 ± 48 s, n = 33) compared with trials in which the emperor moths had their eyespots covered with paint (male-no eye, female-no eye) (317 ± 83 s, n = 22) (t-test: $t_{53} = -2.0$, $p = 0.05$; Fig. 3). Moreover, although 20 of 60 emperor moths were not attacked during the trials, there was no tendency for moths with eyespots intact not to be attacked; when pooling males and females only 50 % of moths (12/24) with eyespots painted over were attacked whereas almost 80 % (28/36) of moths with eyespots intact were attacked (Table 1).

Female emperor moths were approximately 3 times heavier (1.100 ± 0.076 g, n = 13) than males (0.373 ± 0.012 g, n = 10). Additionally, females had longer forewings (36.0 ± 0.9 mm, n = 9) than males (30.7 ± 0.7 mm, n = 14) (t-test: $t = 4.76$, $df = 21$, $p < 0.001$). Pooling the frequencies of surviving emperor moths of the three male treatments and the two female treatments, respectively, females (18 of 24) survived to a higher extent than males (14 of 36) (Fisher's exact test: $p = 0.008$; Table 2). The reason for the higher survival of females was not that they were attacked to a lesser extent, because a similar proportion both sexes were not attacked at all; out of 24 females 9 were not attacked (37.5 %), and out of 36 males 11 were not attacked (30.6 %) (Fisher's exact test: $p = 0.59$; Fig. 4a). However, among the emperor moths that were attacked 9 of 15 females survived, whereas only 3 out 25 males survived (Fisher's exact test: $p = 0.003$) which shows that females were attacked less ferociously by the

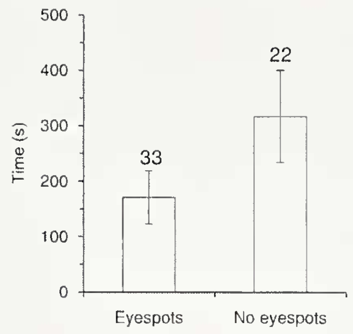


Figure 3. Time until a blue tit first visits an emperor moth with eyespots, or without eyespots. Data are mean ± one standard error (whiskers). Numbers above whiskers are n-values.

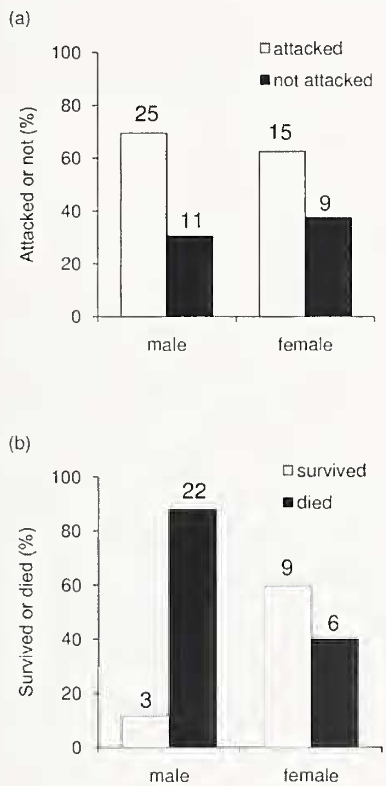


Figure 4. **a**. The proportion of male and female emperor moths that were attacked, or not attacked, during 30-minute trials with blue tits. **b**. The proportion of male and female emperor moths that survived, or were killed, when attacked by blue tits. Data are pooled for the three male, and the two female, treatments, respectively. Numbers above bars are n-values.

Table 1. Sample sizes and the mean time in seconds from the beginning of a trial to when a blue tit first visited the log on the floor (first visit), the time until the emperor moth was attacked for the first time (first attack), and the mean number of attacks. Sample sizes vary because individual blue tits did not necessarily perform all behaviors

Treatment	n	first visit (s) mean±SE
male-eye	9	138 ± 55
male-no eye	12	322 ± 99
male-unmanipulated	12	264 ± 115
female-no eye	10	313 ± 144
female-unmanipulated	12	104 ± 44

blue tits (Fig. 4b). The birds consumed the thorax and the abdomen of the emperor moths that were killed, whereas the wings were left intact.

Discussion

Our results suggest that the blue tits were not intimidated by the conspicuous eyespots on the wings of the emperor moths, as unmanipulated and sham-painted moths with their eyespots intact, were attacked as soon and often as moths with their eyespots painted over. On the contrary, the evidence suggests that the eyespots rather aroused the birds' curiosity, as the birds returned to inspect moths with eyespots sooner compared to moths without eyespots. The results also demonstrate that the larger females survived the attacks from the blue tits better than the males did.

Although the classic literature provides verbal arguments suggesting that conspicuous eyespots on the wings of butterflies and moths can be intimidating to birds (Cott, 1940; Ford, 1955; Edmunds, 1974), this assertion rests on little experimental evidence (Ruxton *et al.*, 2004; Stevens, 2005). Hence, our finding that the eyespots on the wings of the emperor moth were rather ineffective in thwarting bird attacks may not be so surprising, especially given that previous experiments with the eyed hawkmoth produced similar results (Vallin *et al.*, 2007). In this context it is relevant to ask to what extent our experimental setup might have influenced the results, whether birds were less likely to be intimidated when interacting with the moths in a small experimental room? We think not for the simple reason that previous experiments with aposematic and/or with eyespotted insects and blue tits, or great tits (*Parus major*) as predators in the very same experimental room and set-up, have all shown that birds often exhibit obvious signs of fear (Wiklund & Tullberg, 1985; Vallin *et al.*, 2005; 2006, 2007; Kodandaramaiah *et al.*, 2009). Particularly strong evidence for this conclusion comes from earlier experiments in which blue tits were so intimidated by peacocks that only one out of 44 birds dared attack and kill a peacock when the insect had its eyespots intact (Vallin *et al.*, 2005, 2006).

It is more likely that the relatively low intimidating effect of the emperor moths is associated with their lack of efficient deimatic behavior. When comparing the intimidating capacity of the deimatic behaviour of the three eyespotted lepidopterans *I. io*, *S. ocellatus* and *S. pavonia*, it is obvious that that of *I. io* is considerably more effective. The effective defensive behavior of *I. io* may be due to their repeated sequence of opening and closing their wings which makes the eyespots appear and disappear in rapid succession together with their apparent "aggressive" behavior towards the potential predator. The defensive behavior of the emperor moth is more similar to the relatively ineffective one of the eyed hawkmoth, and once attacked emperor moths raise their forewings so that the eyespots on the hind wings are exposed and thereafter keep all of the four eyespots constantly visible performing slow

Table 2. Frequencies of surviving and killed emperor moths classified depending on whether they were attacked or not, after 30-minute trials with wild-caught blue tits.

Treatment	total	attacked	not attacked	alive	dead
male-eye	12	6	6	6	6
male-no eye	12	7	5	6	6
male-unmanipulated	12	12	0	2	10
female-no eye	12	5	7	10	2
female-unmanipulated	12	10	2	8	4

rocking movements as long as they are under attack. However, it is relevant to note that experiments with wings of the eyespotted peacock pansy (*J. almana*) pasted on to a piece of cardboard so as to resemble a butterfly with its wings open, did indeed elicit signs of fear in great tits (Kodandaramaiah *et al.*, 2009). However, for obvious reasons survival of the prey could not be assessed in the *J. almana* experiment, and while the study convincingly demonstrates that large eyespots can elicit fear in a small passerine bird it does not contradict the idea that an effective deimatic behaviour can increase the likelihood of prey survival when attacked.

Another factor that may have influenced the mortality of the emperor moth relates to the experimental setup, that we used two mealworms pinned in close proximity to the emperor moth which had the intended effect of encouraging the bird to approach the mealworms and hence also the moth. This could conceivably either increase, or decrease, the likelihood of bird attack, depending on the personality of the individual bird (Dingemanse *et al.*, 2004; van Oers *et al.*, 2004). Regardless of whether the birds that did not attack the emperor moths can be considered closer to the shyness end of the personality continuum between shyness or boldness, the presence or absence of eyespots on the wings of the moths was apparently irrelevant as the proportion of birds that did not attack the moths did not differ between moth treatments.

Yet another factor that might influence our results could be the extent to which the emperor moths can be considered to match their background. Stevens *et al.* (2008b) showed that the extent to which wing spots reduce predation can be context-dependent; in an experiment using artificial moth-like targets they showed that wing spots reduced predation when on conspicuous "prey" but increased predation on otherwise camouflaged "prey". In our experiment all birds devoured the mealworms and came in close proximity to the emperor moths none of which matched their background and so were rather conspicuous. Although it is difficult to assert objectively, we are convinced that both moths with their eyespots intact and those with their eyespots painted over were clearly discovered by the blue tits. Insofar as eyespots on conspicuous prey reduce bird attacks, this was not the case in our experiment; neither the number of attacks, nor the time to attack, was influenced by whether the emperor moths had their eyespots intact or painted over.

Why did female emperor moths survive significantly better than males? We contend that the most likely explanation is that the females' larger size per se might be an advantage when encountering a small predatory bird such a blue tit which can conceivably be intimidated by a large insect. In a similar fashion, Gamberale and Tullberg (1996) showed that larger individuals (later instars) of the aposematic insect, *Trophidothorax leucopterus* (Heteroptera: Lygacidae), were less often attacked by chickens, *Gallus gallus*, compared with smaller individuals (earlier instars). Additionally, Exnerová *et al.* (2003), observed that equxally large individuals of the aposematic insect, *Pyrrochoris apterus* (Heteroptera: Pyrrhocoridae), were better protected against smaller, compared with larger passerines. Thus, to a predator, larger prey hold a stronger signal value compared with smaller prey and if the signal is associated with something negative, for example bad taste as described above, this will result in a better protected individual. Indeed, in our study the large females survived significantly better than the smaller males when attacked by the blue tits, 60% versus 12%, which suggests that the birds may have been somehow intimidated by the size of their potential prey. The fact that females survive better than males when attacked is also interesting in view of the fact that the hind wings of males are bright orange-red, a color usually conceived of as aposematic, whereas those of the females are grey and the same color as the front wings; however, this apparently did not confer higher survival upon males.

Conceivably the ultimate indicator of predator intimidation would be that the potential insect prey was not attacked at all. In our experiments about 30% of male and female emperor moths were not attacked, which may indicate that the blue tits were intimidated by their eyespots or their size or a combination of the two, in relation to the "personality" of the individual bird, as discussed above. Another possible explanation for why approximately one out of three blue tits did not attack emperor moths could be that these insects represent unfamiliar prey, and so may escape attack because of neophobia (cf. Marples *et al.*, 1998; Marples & Kelly, 2001).

In our experiment birds visited the log on the floor after a shorter period of time in trials with emperor moths with eyespots intact compared with emperor moths with eyespots painted over. Two hypotheses could explain this result. First, studies on humans (Attneave, 1954), pigeons (Delius & Nowak, 1982) and honeybees (Horridge, 1996) have shown that symmetrical patterns, such as eyes, are easier to detect, associate and remember compared with other patterns. Thus, it may be the case that emperor moths with exposed eyespots are simply detected earlier in trials, and consequently, the birds fly down to the log to make their initial assessment of the situation earlier.

The other possible explanation is that the eyespots of the emperor moth actually resemble those of a real predator, for example a small owl, which would present a real threat to the attacking bird (Cott, 1940; Edmunds, 1974; Ruxton, 2005, but see Stevens, 2005, 2007). Should this be the case, the result could also be explained in terms of predator inspection where a prey actively approaches a predator (Curio, 1978). The rationale behind this behavior is that a potential prey can gather information about the predator and at the same time convey the message that the predator has been spotted (e.g. Magurran, 1986; FitzGibbon, 1994).

In conclusion, this study of the efficiency of conspicuous eyespots as a primary defense in a living lepidopteran does not support the idea that eyespots on the wings of the emperor moth have an intimidating function and deter attacks from small birds. Rather, the evidence suggests that large eyespots, in this species, may be associated with a cost, because potential predators have their attention aroused rather than being intimidated by the prey's display. Finally, our results suggest that the size of the insect prey may have an intimidating function and can deter, or make less ferocious, bird attacks on larger moths and butterflies.

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